

5 June 2005

**TO:** Dr. Peter Plage, USF&WS, 755 Parfet St., Suite 361, Lakewood, CO 80215, peter\_plage@fws.gov.  
**FR:** Douglas A. Kelt, Professor of Wildlife Biology, Dept. of Wildlife, Fish, & Conservation Biology, University of California, Davis.  
**RE:** Review of documents pertaining to delisting of Preble's meadow jumping mouse (*Zapus hudsonicus preblei*).

Dear Dr. Plage,

Following are my comments on the USF&WS's "12-Month Finding on a Petition to Delist the Preble's Meadow Jumping Mouse (*Zapus hudsonius preblei*) and Proposed Delisting of the Preble's Meadow Jumping Mouse." In the cover letter sent by Susan Linner I was asked to consider (but not be limited to) two questions:

- 1. Do I support the conclusion that the best scientific and commercial information available indicates that Preble's is not a discrete taxonomic entity?**
- 2. Could I support finalizing the proposal to delist *Z. h. preblei* based on the information currently available? If not, what additional information is needed?**

Towards this end I have read the 12-month finding published by UFW&WS (Federal Register 70(21):5404-5411), the report that Ramey et al. (2004) provided to the Governor of Wyoming and to USFWS, and the comments on this report by nine external reviewers. I have also read, to varying degrees of thoroughness, previous studies on this mouse and on related issues, most of which were provided by you on a CD. Finally, I encountered and read one additional manuscript by R. R. Ramey II and colleagues, and currently in press in *Animal Conservation*, which summarizes their work on *Z. h. preblei* but employs additional data beyond that available in Ramey et al. (2004).

In the spirit of full disclosure, recognize that I am an ecologist with particular emphasis on community to biogeographic scales. I am not a systematist although mammalian taxonomy is a hobby, and I am not strongly versed in contemporary methods of phylogenetics or molecular systematics. I was pleased to see that some of my well-respected colleagues in this arena were invited to comment on Ramey et al. (2004). That all said, I do consider myself sufficiently versed in these areas that I can integrate the comments of these 9 external reviewers, and draw my own independent conclusions on the extent to which Ramey et al. (2004) and other materials resolve the questions posed above.

Onward to the questions at hand.

- 1. Do I support the conclusion that the best scientific and commercial information available indicates that Preble's is not a discrete taxonomic entity?**

The best scientific and commercial information available certainly gives reason to question the distinctiveness of Preble's mouse. However, I find myself agreeing with S. Oyler-McCance's

comment that Ramey et al. (2004) “provides a great data set from which to **begin** to answer the question at hand” (emphasis in the original). And, while G. White notes that “one can never state that 2 items are identical . . . because the one critical difference between [them may not have been] measured or detected in the analysis” the flaw in this argument is that strict adherence to this rule would preclude allocation of *any* two individuals to a species. Systematics and taxonomy proceed on the principal that cohesive groups of individuals are allocated to species (or other taxonomic units) on logical grounds, and failure to distinguish among individuals or populations is used to group these individuals or populations as species. From the data available, Ramey et al. (2004) make a strong argument that *Z. h. preblei* is not clearly distinguishable from other subspecies of *Z. hudsonicus*. Given this, the real questions at hand are whether or not the data available are adequate to make this assessment, and if the most prudent course of action is to accept this “best assessment” or, if these data are deemed insufficient, to defer until sufficient data are available such that the allocation of populations of *Z. h. preblei* is more clear. My personal preference would be to defer, and to urge scientists to address this issue more clearly and especially, in the peer-reviewed literature. One problem with the taxonomy of *Z. hudsonius* appears to be the fact that key papers or analyses, from Jones 1981 to J. Cook (unpublished) to Ramey et al. (2004) have not been exposed to peer review and subsequent scientific scrutiny. Thus, it is not clear to what extent these conclusions will hold up under the microscope of peer review.

M. Douglas noted that discriminant analyses are not entirely appropriate for morphological assessment as they require *a priori* allocation of all specimens into one group. A related point is that DFA is a methodological approach that attempts to maximize differences between *a priori* determined groups; thus, it should maximize the resolution between these groupings if such differences exist. The fact that such differences proved trivial (only 48% of specimens classified correctly in a post-facto test) supports the lack of morphological distinctiveness between these groups. An alternative and complementary approach would be principal components analysis, which is a related multivariate technique that does not require *a priori* allocation of specimens to any group, and makes no attempt to maximize distinctiveness among groups of variables. Multivariate analysis of variance can then be applied to these data to assess distinctiveness among taxa, but again, without *a priori* attempting to maximize these differences. I am fairly comfortable with the DFA results, however, since they seem particularly clear in failing to distinguish between taxa that were identified by geographical range (e.g., corresponding to the range of particular subspecies). Interestingly, Ramey et al. (in press) subsequently applied *both* PCA and DFA to Preble’s and related subspecies, finding substantial overlap among all three subspecies, and recommending synonymizing both *Z. h. preblei* and *Z. h. intermedius* under *Z. h. campestris*.

I also concur with M. Douglas that Ramey et al. (2004, in press) should not have constrained themselves to using only the cranial characters that Krutsch used. If additional measurements would be useful, why not incorporate them? This relates to some degree with comments by other reviewers who perceived a bias or agenda in the structure and style of Ramey et al. (2004). Evidently no attempt was made to evaluate the utility of additional morphological characters, which I consider unfortunate and somewhat short-sighted. However, the PCA presented in Ramey et al. (In press) convinces me of the lack of morphological differences between *Z. h. preblei*, *Z. h. intermedius*, and *Z. h. campestris*.

Finally, more than one of the 9 reviewers noted the glaring absence of ecological data for comparing *Z. h. preblei* to other populations and taxonomic subunits of *Z. hudsonius*. This is indeed highly unfortunate, although in all fairness I believe that the genetic and morphologic analyses are more convincing than ecological differences might be. I state this because ecological differences – such as differences in microhabitat use or in demographic parameters – could very well be a reflection of differences in the habitat in which this taxon occurs. Thus, of the three types of information – genetic, morphologic, ecologic – I would place the greatest intellectual stock in the genetic analyses, and the least in the ecologic analyses, in determining the validity of a population as a unique evolutionary unit such as a subspecies or evolutionarily significant unit (ESU).

In summary, the available data do not appear supportive of the taxonomic distinctiveness of *Z. h. preblei*, but it is not clear that further data – most notably a broader range of mtDNA sequences, incorporation of nuclear DNA, and possibly a more comprehensive morphological and ecological assessment of these populations – might not lead to different results. Indeed, further study would be highly useful in “clinching” this scientific conclusion. Thus, the “best available information” does not support distinguishing *Z. h. preblei*, but the “best available information” appears slightly limited.

## **2. Could I support finalizing the proposal to delist *Z. h. preblei* based on the information currently available? If not, what additional information is needed?**

Philosophical background. My general philosophy on issues of threatened and endangered species is that they should be given the benefit of the doubt until it is indeed clear that they are not threatened. Because the “best available information” is somewhat limited in the case of Preble’s mouse, and because of the lack of virtually any ecological information, the lack of a more comprehensive morphological study, and the limited mtDNA sequence and absence of any nuclear DNA data, I believe that we should give the mouse the benefit of the doubt while time is available. Once this or any other taxon is de-listed, the process of re-listing – should this be necessary – would be an arduous and litigious process that would consume extensive resources (both personnel and financial) by USF&WS. The “ratchet effect” (Ludwig et al. 1993, Botsford et al. 1997) describes the inevitable slide toward loss of habitat and biodiversity as decisions are made using “best available information” when that information is insufficient. With an additional development or water project sanctioned, lands are irrevocably lost for conservation means, and we gradually “ratchet down” our options for future management of native species or habitats.

The *cost of delisting* Preble’s mouse is the cost of potentially committing a type 2 error – failing to distinguish between two entities should they in fact be distinct. The limited base pair sequence available to Ramey et al. (2004) was noted by some reviewers as a cause for questioning the power of their assessment that *Z. h. preblei* is not distinct from other populations or subspecies of *Z. hudsonius*. If this concern is valid, then the failure to distinguish *Z. h. preblei* from other taxa may reflect a lack of sufficient information rather than on a true lack of distinction. USFWS (in the 12-month finding; p. 5408) noted that “Although a larger number of base pairs is desirable . . . mtDNA studies often utilize less than 1,000 base pairs.” While this

may be true, the cards we play with when evaluating the fate of a putative evolutionary lineage is different, and therefore should be held to a higher level of proof, than that employed in standard systematic studies, where the cost of an error may be merely a misunderstanding of phylogenetic relations.

In contrast, the *cost of declining to delist* Preble's mouse can be measured primarily in terms of economic terms (i.e., limitations to consumptive use of lands currently considered to be Critical Habitat) and potentially in political capital (anger towards USF&WS and its personnel; increased public questioning of the Endangered Species Act and possibly political movement to dilute the Act). These are undoubtedly important considerations. The ESA was developed, however, to protect species under the seemingly interminable onslaught of habitat consumption by humans, and presumably it was hoped that this would protect species by setting aside lands. The counter to this is that all laws are subject to repeal, and if human needs for habitat are not restrained we are certain to "need" lands tomorrow that we set aside for "permanent protection" yesterday.

Thus, the decision to de-list rests on a cost-benefit analysis of two issues – potential damage to Preble's mouse if we de-list and subsequently determine that we are wrong, vs. limited opportunities for consumptive uses of Critical Habitat and potential political damage to the ESA and USF&WS if we de-listing is avoided, and we lack sufficient evidence to document the unique status of Preble's mouse.

Assessment. Available genetic analyses do not support recognizing *Z. h. preblei* as a distinct entity. Morphological analyses presented by Ramey et al. (2004, In press) concur with the genetic analyses. Ecological data are largely lacking, but given the similarities among all *species* of *Zapus* in habitat selection, diet, etc., it seems highly unlikely that *Z. h. preblei* will be found to differ ecologically from other subspecies of this species.

D. Hafner noted in his review of Ramey et al. (2004) that even if *Z. h. preblei* is a junior synonym of *Z. h. campestris*, the latter entity is considered to be vulnerable, and so the broader "*campestris* + *preblei*" entity would remain of conservation concern.

Ramey et al. (2004) noted that their study required only three weeks of effort and approximately \$7,000 to complete. In the broader scope, it is exactly this type of situation that begs for a revised biological inventory of the United States, although economic realities are certain to preclude such a venture in the near future. It is unclear, however, whether the greater financial output lies in the continual administrative and legal expenses associated with evaluating each entity currently or potentially listed as threatened or endangered, or in interfacing with mammalian systematists nationwide in a comprehensive evaluation of the taxonomic and phylogenetic status of these species before litigation and administrative hurdles are encountered.

I concur with M. Douglas that revisiting old analyses without new data, and without fully resolving questions of analytical (or statistical) power has the makings of a grave error. She and other reviewers noted a number of potentially serious problems with Ramey et al. (2004). That more reviewers were generally favorable towards Ramey et al. (2004) than were critical of it does not avoid the fact that some very serious limitations have been noted by some reviewers, most notably Conner, Douglas, Meaney, Oyler-McCance, and White, and if these limitations are

valid then the broader issue of the distinctiveness of *Z. h. preblei* is far from resolved with the report by Ramey et al. (2004; or by Ramey et al. In press).

In summary, however, the available morphological and genetic data provide no strong support for recognizing *Z. h. preblei* as a taxonomic entity, and I believe they suggest that this taxon is indeed not distinct from other populations of *Z. hudsonius*. Consequently, I would support delisting *Z. h. preblei* under the current circumstances.

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Ramey, R. R., II, H-P. Liu, C. W. Epps, L. M. Carpenter, and J. D. Wehausen. In press. Genetic relatedness of the Preble's meadow jumping mouse (*Zapus hudsonius preblei*) to nearby subspecies of *Z. hudsonius* as inferred from variation in cranial morphology, mitochondrial DNA, and microsatellite DNA: implications for taxonomy and conservation. *Animal Conservation*.



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July 15, 2005

To whom it may concern:

Thank you for the opportunity to review this report. I commend the authors both for the hypothesis-testing approach and the integration of genetic and morphological data. While I think the report raises several interesting questions about the “uniqueness” of *Zapus hudsonicus preblei*, I also have several concerns. In particular, additional data is necessary to confirm and/or refute these preliminary results.

General comments:

1. Amplification of museum DNA is often prone to contamination. Most labs conduct all PCR-based experiments in fume hoods and in a separate laboratory for pre- and post-PCR methods. Negative controls are run at every stage from DNA extraction to sequencing. The details of the procedures used here are needed, including specific explanations as to how contamination was controlled and checked. It would not be un-reasonable to ask that a second lab (which does not work on *Zapus*) to repeat these results.
2. There are several concerns of relying on a small region of the mitochondrial genome.
  - a. Mitochondrial markers represent only a single genetic locus. It is clear that often different regions of the genome have different coalescent histories, some of which don't agree with the “true” species history. I would argue that systematic studies based solely on a single genetic marker are suspect.
  - b. In addition, this entire analysis is based on only 355 basepairs with only a few informative nucleotide sites.
  - c. Mitochondrial genomes can often be subject to introgression, where rare or historical hybridization can lead to an mtDNA haplotype invading the nuclear genome of another species/subspecies/population, resulting to incorrect conclusions about population structure and taxonomic validity if no additional markers are used.

Importantly, concerns (b) and (c) are unlikely to play a significant role here given the pattern of nucleotide variability observed in *preblei* mtDNA, nonetheless they should be directly addressed in this report. Much more relevant are concerns of contamination and the use of only a single genetic locus to make conclusions about population-level processes. The inclusion of additional markers, such as microsatellite loci, which are small, rapidly-evolving markers and ideal for degraded museum DNA, would add important unlinked loci both for phylogenetic analysis and inference of population structure.

3. I have several comments in regards to the interpretation of the population genetic data in the Discussion (page 9).

- a. Fst estimates can be inflated if overall levels of genetic diversity differ greatly between the populations in question. However, it is of interest to know how inflated these estimates are given the differences in nucleotide variability observed here.
- b. Nucleotide diversity is a function of effective population size ( $N_e$ ) and mutation rate ( $u$ ). Low levels of nucleotide variability in *Z. h. preblei* can be due to historically small population size, rather than simply “not being a long term resident”.
- c. Haplotype sharing does not always indicate current genetic exchange. An alternative hypothesis is that there has not been enough time for lineage sorting to be complete, suggesting that the populations have been isolated relatively recently (without invoking current migration or gene exchange).

4. Why were only 33 *Z. h. preblei* used in the discriminate analysis? I would like to see more of the morphological data and details included in a table(s), so that reader would be better able to evaluate the conclusions of the morphological analyses.

5. The examination of cranial measurements replicates previous studies of *Zapus*. However, if one is interested in learning if there are any ecological or adaptive differences between subspecies, examining “neutral” cranial characters may not be the best approach. I would recommend also analyzing ecologically relevant morphological traits, such as baculum morphology, which is known to evolve rapidly between species and variation may be directly related to reproductive isolation.

6. In the conclusions, it is stated that “three lines of evidence” were used to test the taxonomic validity of *Z. h. preblei*. This is an overstatement. The third line is pure conjecture and no quantitative data was collected. A spectrophotometer should be used to quantitate differences in pelage reflectance. It is clear that avian predators, for example, have a very different visual system than mammals, and humans in particular. So, the lack of variation that we perceive may be relevant for avian predators.

7. Lack of published evidence that the subspecies under question are ecologically distinct is not evidence that there are no ecological differences.

8. Additional references need to be added throughout this report. The background information and supporting references are lacking.

To address specific questions:

**1) Do you support the conclusion that the best scientific and commercial information available indicates that Preble's is not a discrete taxonomic entity?**

At present, there is not enough data to support this conclusion.

**2) Could you support finalizing the proposal to delist Preble's based on the information currently available or is other information needed.**

I could not support a final decision based on these limited data. In particular, I recommend the following data and/or information is necessary:

- (1) description of molecular methods and relevant controls for ancient DNA work,
- (2) additional molecular markers such as microsatellite loci,
- (3) ecological information comparing *Z. h. preblei* and *Z. h. campestris*.

Please do not hesitate to contact me if you have any questions.

Sincerely,

Hopi Hoekstra, Ph.D.





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Mr. Peter Plage  
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16 June 2005

**Subject: Peer Review of 12-Month Finding on a Petition to Delist the Preble's Meadow Jumping Mouse (*Zapus hudsonius preblei*) and Proposed Delisting of the Preble's Meadow Jumping Mouse (ES/CO: T&E: Preble's Delisting; Mail Stop 65412)**

Dear Mr. Plage:

The Conservation Biology Institute is a nonprofit research and planning institution that provides scientific guidance and review for efforts to conserve biological diversity, such as habitat conservation plans and endangered species recovery plans. I am a wildlife conservation biologist with degrees in biology (BS), wildlife management (BS and MS), and ecology and evolutionary biology (PhD). I have roughly 25 years research and planning experience with rare, threatened, and endangered species in the western U.S. Although I am not a classically trained mammalogist, my taxonomic focus has generally been mammals, especially rodents and carnivores. Most pertinent to this review, I have performed and coordinated applied research to further the recovery of endangered rodent species, including the Stephens' kangaroo rat (*Dipodomys stephensi*) and Pacific little pocket mouse (*Perognathus longimembris pacificus*) (Spencer, in press). Although I am not a geneticist or morphologist, I have some working experience with the genetic and taxonomic concepts and analytical techniques discussed in the subject documents, including as a coauthor on a genetic review of the little pocket mice of California using mitochondrial DNA (Swei et al. 2003).

I have reviewed the subject document (Finding on Petition ...and Proposed Delisting of the Preble's Meadow Jumping Mouse, *Zapus hudsonius preblei*; hereafter *proposal*). I also reviewed most of the scientific papers, reports, and reviews cited in the proposal



(although lack of time precluded detailed review of all documents). I organize my review using the two main questions I was asked to address.

1. Do you support the conclusion that the best scientific and commercial information available indicates that Preble's is not a discrete taxonomic entity?

Yes, the weight of scientific evidence I reviewed appears to support that Preble's meadow jumping mouse (*Z. h. preblei*) is not a distinct subspecies and appears to be synonymous with *Z. h. campestris*. However, I share concerns raised by others about over-extrapolation of some conclusions in the principle scientific report cited to support this finding (Ramey et al. 2004). Specifically, although no subspecific differences were detected *with the measures employed to date* (limited mitochondrial DNA analysis and skull morphometrics), I disagree with Ramey et al. (2004) that (1) failure to detect a difference with these measures proves sameness (an apparent violation of "the scientific method" preached by Ramey et al. 2004); (2) that combining *Z. h. preblei* and *Z. h. campestris* means that former *Z. h. preblei* populations cannot comprise a Distinct Population Segment (DPS); and, especially (3) that a combined *preblei-campestris* subspecies is of no conservation concern. As pointed out by other peer reviewers, these are clear over-extensions of the Ramey et al. (2004) analyses, and they have little if any scientific support. Nevertheless, I must conclude, based on a balanced review of all available evidence, that the *taxonomic* conclusion of Ramey et al. (2004) is probably correct.

2. Could you support finalizing the proposal to delist Preble's based on the information currently available? If not, what additional information is needed?

Although this answer should ideally be based purely on objective science, it is impossible to disentangle it completely from legal and political implications. Given uncertainty about whether *Z. h. preblei* populations comprise a DPS, or whether a combined *preblei-campestris* subspecies is still threatened with extinction (Hafner in litt. 2004), delisting has the potential to do irrevocable harm to biodiversity.

As a conservation scientist that works at the interface between science and policy, I am personally aware of instances where removal or temporary withholding of protections for a species leads to aggressive efforts by those who fear economic harm from protections to rid their properties of the species at issue (e.g., by poisoning or clearing of habitat in anticipation of new or re-imposed protections). I therefore am hesitant to conclude that finalizing the proposal based on available information is warranted or prudent given this potential for irrevocable harm and remaining uncertainty about the conservation value of *Z. h. preblei* populations. Important information gaps remain, especially concerning the potential for adaptive genetic variation among disjunct populations of *Z. hudsonius*. Addressing this requires (at least) further genetic analysis using nuclear DNA coupled with research on morphological, physiological, behavioral, or ecological similarities or differences between *Z. h. preblei* and other subspecies.



I agree with Riddle (in litt. 2004) that, given the biogeographic structure of *Z. hudsonius* populations, substantial evolutionary subdivisions are unlikely to be found with nuclear DNA given that they were not detected with mtDNA. Nevertheless, there remains uncertainty about potential adaptive differences among populations. As well put by Riddle (in litt. 2004): "...these populations could well contain a set of ecological traits that have selective advantage in extreme environments and therefore are unique and interesting (perhaps irreplaceable) within the context of the species as a whole." In other words, there could well be adaptive variation (and one or more DPSs) essential to conservation and recovery of these rare jumping mice, particularly in light of ongoing rapid climate change.

The proposal notes that the Service expects additional genetics information, including nuclear DNA results, "within the next year." *At the very least, I strongly urge the Service to await such results before finalizing this proposal.* It is possible that there are adaptive genetic differences between *Z. h. preblei* and other subspecies that have yet to be found, and mtDNA is a very blunt instrument for detecting adaptive differences, even where there are strong ecological factors driving adaptive change (see e.g., Swei et al. 2003). Crandall (in litt. 2004), although strongly endorsing Ramey et al.'s (2004) conclusions, presents the illuminating example of polar bears and brown bears—which, despite obvious adaptive differences (at the full species level) cannot be differentiated as distinct clades using neutral genetic markers!

Ramey et al.'s (2004, p.9) simplistic conclusion that "no quantitative evidence exists to reject the hypothesis of historic or recent ecological exchangeability (ecological similarity) between *Z. h. preblei* and *Z. h. campestris*" cannot go unchallenged. This is one of several misleading examples in the report of treating "failure to detect" as "proof positive." (It translates roughly to "no one looked, so no one saw.") As noted by other reviewers, Ramey et al. (2004) did not support this ecological conclusion with any analyses or references, and did not describe what environmental variables they considered. Note that this is a small, hibernating species, and that the geographic range of a combined *preblei-campestris* subspecies spans broad and pertinent environmental gradients (especially north-south climate variation). There could well be adaptive variation among populations in, for example, the physiological mechanisms controlling hibernation. Such traits would be controlled by nuclear genes not addressed by analyses of mtDNA and would not necessarily be detected by looking at skull morphology.

Continuing on this point, I don't find the limited morphological analyses performed by Ramey et al. (2004) (using only skull dimensions) at all conclusive concerning subspecific designations, let alone adaptive variation. Subspecies may be differentiated by, for example, adaptive variation in pelage characteristics. Has anyone considered an objective, quantitative analysis of color differences between putative subspecies? Krutch (1954) described pelage differences among subspecies, which were vaguely challenged by Ramey et al. (2004). Given the controversy, a full, quantitative analysis seems in order. This could easily be done using colorimeter readings from specific body regions on museum specimens.



## Conclusions

Although I find the taxonomic conclusion in the proposal likely sound (that *Z. h. preblei* and *Z. h. campestris* are one subspecies) taxonomy alone does not determine conservation value of species populations. I strongly endorse the stated intentions of the Service that, prior to any final, affirmative decision on delisting *Z. h. preblei*, the Service will evaluate (1) the status and threats to the combined *Z. h. campestris* entity in all or a significant portion of its range, and (2) the potential for the Preble's portion of *Z. h. campestris* range to qualify as a DPS. I urge completion, *and publication*, of nuclear DNA analyses. I further suggest a much more thorough review of ecological similarities or differences among populations of the *Z. h. campestris* entity with particular attention to environmental gradients that may drive adaptations (especially in behavioral physiology). Finally, I suggest further morphological analyses of museum specimens, including use of quantitative colorimeter readings of pelage.

Although, following the letter of the law, delisting based on available information may be warranted, it does not seem at all prudent given the very real uncertainties about potential adaptive variation among populations and its potential importance to the continued existence of the subspecies (especially in light of climate change). Delisting could do irrevocable harm pending results of further analyses.

I hope you find these comments useful.

Sincerely,

A handwritten signature in blue ink, appearing to read "Wayne D. Spencer", written over a light blue grid background.

Dr. Wayne D. Spencer  
Senior Conservation Biologist



## Literature Cited

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